



## A new species of Andean microteiid lizard (Gymnophthalmidae: Cercosaurinae: *Pholidobolus*) from Peru, with comments on *P. vertebralis*

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**Abstract.**—Based on morphological and molecular evidence, herein is reported the discovery of a new species of *Pholidobolus* from the Andes of northwestern Peru. The new species is known from the montane forests of Cajamarca and Lambayeque departments, at elevations of 1,800–2,300 m. It differs from other species of *Pholidobolus* in lacking prefrontal scales and having both strongly keeled dorsal scales and a diagonal white bar in the rictal region. Additionally, it is shown that records of *P. vertebralis* from Peru are based on misidentified specimens. The southernmost distribution records of *P. vertebralis* are from northwestern Ecuador. Also, an updated identification key for species of *Pholidobolus* is provided.

**Key words.** Andes, hemipenial morphology, lizards, *Pholidobolus vertebralis*, systematics

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### Introduction

Lizards in the New World family Gymnophthalmidae Merrem 1820 are small, with elongate bodies and relatively short limbs, which are reduced in various degrees in some species and nearly absent in others (Pianka and Vitt 2003). Gymnophthalmidae comprises 47 taxa traditionally ranked as genera with 253 species (Uetz and Hošek 2016). The diversity of gymnophthalmid lizards is high in both the Amazonian rainforests and the Andes (Presch 1980). Some genera like *Euspondylus*, *Gelanesaurus*, *Macropholidus*, *Pholidobolus*, *Petracola*, *Proctoporus*, and *Riama* are restricted to the Andes and reach high elevations. For example, *Proctoporus bolivianus* can be found at 4,080 m in Peru (Duellman 1979).

Species of *Pholidobolus* occur between 1,800 and 4,000 m along the northern Andes from northern Peru in the Huancabamba Depression to extreme southern Colombia (Torres-Carvajal and Mafla-Endara 2013). Montanucci (1973) defined *Pholidobolus* using morphological characters and recognized five species: *P. affinis* (Peters 1863), *P. annectens* (Parker 1930), *P. macbrydei* Montanucci 1973, *P. montium* (Peters 1863), and *P. prefrontalis* Montanucci 1973. Twenty-three years later Reeder (1996) described *P. huancabambae*. However, recent taxonomic changes have been proposed based on molecular phylogenetic evidence. Two species of *Pholidobolus*, *P. annectens*, and *P. huancabambae*, were allocated in its sister clade, *Macropholidus* (Torres-Carvajal and Mafla-Endara 2013). More recently, “*Cercosaura*” *dicra* (Uzzell, 1973) and “*C.*” *vertebralis*

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O'Shaughnessy 1879 were found to be members of *Pholidobolus* (Torres-Carvajal et al. 2015), increasing the number of species in this genus to seven, including the recently described *P. hillisi* (Torres-Carvajal et al. 2014).

Morphologically, members of *Macropholidus* and *Pholidobolus* can be distinguished from each other by the presence of a single palpebral disk in the lower eyelid in *Macropholidus* (divided in *Pholidobolus*), and the lack of a lateral fold in *Macropholidus* (present in *Pholidobolus*). Nonetheless, the phylogenetic position of *P. anomalus* Müller 1923, a geographically disjunct species from southern Peru, is still uncertain (Montanucci 1973; Reeder 1996; Torres-Carvajal and Mafla-Endara 2013).

Herein, based on morphological and previously published molecular evidence (Torres-Carvajal et al. 2015 and 2016), we report the discovery of a new species of *Pholidobolus* collected in different field trips to montane forests in the Andes of northwestern Peru. This discovery increases the number of species of *Pholidobolus* to eight.

## Materials and Methods

All type specimens of the new species described in this paper were deposited in the herpetological collection of Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru. Specimens used for comparisons are housed at Museo de Zoología, Pontificia Universidad Católica de Ecuador, Quito (QCAZ) (Appendix I). The following measurements were taken with digital calipers and recorded to the nearest 0.1 mm, except for tail length (TL), which was taken with a ruler and recorded to the nearest millimeter: head length (HL), head width (HW), shank length (ShL), axilla-groin distance (AGD), and snout-vent length (SVL). Sex was determined either by dissection or by noting the presence of everted hemipenes. We follow the terminology of Reeder (1996) for the description of the holotype and scale counts, and Montanucci (1973) for the diagnosis. Morphological data from other species of *Pholidobolus* were taken from the literature (Montanucci 1973; Reeder 1996; Torres-Carvajal et al. 2014).

The left hemipenis of the holotype (CORBIDI 12734) was prepared following the procedures described by Manzani and Abe (1988), modified by Pesantes (1994) and Zaher (1999). The retractor muscle was manually separated and the everted organ filled with stained petroleum jelly. The organs were immersed in an alcoholic solution of Alizarin Red for 24 hours in order to stain eventual calcified structures (e.g., spines or spicules), in an adaptation proposed by Nunes et al. (2012) on the procedures described by Uzzell (1973) and Harvey and Embert (2008). The terminology of hemipenial structures follows previous literature (Dowling and Savage 1960; Savage 1997; Myers and Donnelly 2001, 2008; Nunes et al. 2012).

## Results

**Systematics:** The taxonomic conclusions of this study are based on the observation of morphological features and color pattern, as well as on previously inferred phylogenetic relationships based on molecular data (Torres-Carvajal et al. 2015). We consider this information as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998, 2007).

### *Pholidobolus ulisesi* sp. nov.

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Figs. 1–3.

*Cercosaura vertebralis*—Doan and Cusi 2014 (part): 1,195–1,200.

*Pholidobolus* sp.—Torres-Carvajal et al. 2015: 286.

*Pholidobolus* sp.—Torres-Carvajal et al. 2016: 70 (Fig. 2).

**Holotype:** CORBIDI 12734, an adult male from Bosque de Huamantanga (5°39'48.09" S, 78°56'35.8" W), at 2,211 m elevation, Huabal district, Jaén province, Cajamarca department, Peru, collected on 7 March 2013 by P.J. Venegas.

**Paratypes (17):** CORBIDI 12740–46 juveniles, CORBIDI 12735–36, 12739 adult males, CORBIDI 12737–38 adult females, all collected with the holotype; CORBIDI 00871–73, an adult female, an adult male and a juvenile, respectively, from El Chaupe (5°14'8.16" S, 79°5'56.58" W), at 2,016 m elevation, Namballe district, San Ignacio province, Cajamarca department, Peru, collected by M. Doherty on 24 August 2008; CORBIDI 14889, an adult female, and CORBIDI 14896, a juvenile, from San Felipe de Jaén (5°45'10.854" S, 79°14'19.881" W), at 2,641 m elevation, Jaén province, Cajamarca department, Peru collected by K. Garcia on 26 September 2014.

**Photo voucher specimen:** Cañaris (6°03'26.18" S, 79°16'00.35" W), at 2,318 m elevation, Ferreñafe province, Lambayeque department, Peru, captured and released by P.J. Venegas on 25 May 2007 (Fig. 3D).

**Diagnosis:** *Pholidobolus affinis*, *P. dicrus* (Fig. 4A), *P. hillisi* (Fig. 4B), *P. prefrontalis*, and *P. vertebralis* (Fig. 4C) differ from the new species in having prefrontal scales. *Pholidobolus montium* and *P. macbrydei* have striated and quadrangular dorsal scales (strongly keeled and hexagonal in *P. ulisesi*), and lack the conspicuous narrow, pale brown, vertebral stripe present in *P. ulisesi*. In addition, the new species has fewer dorsal scales (28–31,  $\bar{x}$





**Fig. 1.** Holotype of *Pholidobolus ulisesi* sp. nov. (CORBIDI 12734; male, SVL = 45.5 mm) in dorsal (**top**) and ventral (**bottom**) views. Photographs by OTC.

= 29.75) than *P. affinis* (45–55), *P. montium* (35–50), *P. prefrontalis* (37–46), and *P. macbrydei* (31–43).

**Characterization:** (1) Two or three supraoculars, anteriormost larger than others; (2) prefrontals absent; (3) femoral pores absent in both sexes; (4) two to six opaque lower eyelid scales; (5) scales on dorsal surface of neck striated, becoming strongly keeled between forelimbs and tail; (6) two or three rows of lateral granules at midbody; (7) lateral body fold present; (8) usually two rows of keeled ventrolateral scales on each side; (9) dorsum dark brown with a distinct pale brown middorsal stripe, slender at midbody, becoming grayish brown towards the tail; (10) labial stripe white becoming cream or pale brown along ventrolateral region; (11) sides of body dark brown; (12) cream stripe along forearm; (13) a distinct diagonal white bar with dark brown edges on each side of the mandible, extending from sixth infralabial to proximal preangular; (14) orange spots on sides of body, usually above forelimb and the base of tail in adult males.

**Description of holotype:** Adult male (CORBIDI 12734; Fig. 1–3A); SVL 45.5 mm; TL 104 mm; dorsal

and lateral head scales juxtaposed, finely wrinkled; rostral hexagonal, 2.03 times as wide as high; frontonasal quadrangular, wider than long, longer than frontal, laterally in contact with nasal, loreal, and first superciliary; prefrontals absent; frontal pentagonal, longer than wide, slightly wider anteriorly, in contact with frontonasal and supraocular I on each side; frontoparietals hexagonal, longer than wide, with medial suture, each in contact laterally with supraoculars I and II; interparietal roughly heptagonal, its lateral borders parallel to each other; parietals slightly smaller than interparietal, pentagonal and positioned anterolaterally to interparietal, each in contact anteriorly with supraocular II and dorsalmost postocular; postparietals three, medial scale smaller than laterals; supralabials seven, fourth longest and below the center of eye; infralabials five, fourth below the center of eye; temporals enlarged, irregularly pentagonal or hexagonal, juxtaposed, finely wrinkled; two finely wrinkled supratemporals, dorsal conspicuously larger than ventral one; nasal divided, irregularly tetragonal, longer than wide, in contact with rostral anteriorly, first and second supralabials ventrally, frontonasal dorsally, loreal posterodorsally and frenocular posteroventrally; nostril on ventral aspect





**Fig. 2.** Head of the holotype of *Pholidobolus ulisesi* sp. nov. (CORBIDI 12734) in dorsal (A), ventral (B), and lateral (C) views. Photographs by OTC.

of nasal, directed lateroposteriorly, piercing nasal suture; loreal rectangular; frenocular enlarged, in contact with nasal, separating loreal from supralabials; supraoculars two, with the first being the largest; four elongate superciliaries, first one enlarged, in contact with loreal; palpebral disk divided into two pigmented scales; suboculars three, elongated and similar in size; three postoculars, ventral one smaller than the others; ear opening vertically oval, without denticulate margins; tympanum recessed into a shallow auditory meatus; mental semicircular, wider than long; postmental pentagonal, slightly wider than long, followed posteriorly by three pairs of genials, the anterior two in contact medially and the posterior one separated by postgenials; all genials in contact with infralabials; gulars imbricate, smooth, widened in two longitudinal rows; gular fold incomplete; posterior row of gulars (collar) with two enlarged scales medially, larger than the anterior gulars.

Scales on nape similar in size to dorsals, except for the anteriormost that are widened; scales on sides of neck small and granular; dorsal scales elongated, imbricate,

arranged in transverse rows; dorsal scales on nape striated, becoming progressively keeled from forelimbs to tail; number of dorsal scales between occipital and posterior margin of hind limbs 30; dorsal scale rows in a transverse line at midbody 19; dorsals separated from ventrals by two longitudinal rows of large keeled scales on each side; longitudinal fold between fore and hind limbs present; ventrals smooth, wider than long, arranged in 21 transverse rows between collar fold and preanals; six ventral scales in a transverse row at midbody; subcaudals smooth; limbs overlap when adpressed against body; axillary region composed of granular scales; scales on dorsal surface of forelimb striated, imbricate; scales on ventral surface of forearm small and imbricate, those on ventral surface of arm granular; two thick, smooth thenar scales; supradigitals (left/right) 3/3 on finger I, 6/6 on II, 8/8 on III, 9/9 on IV, 6/6 on V; supradigitals 3/3 on toe I, 6/6 on II, 10/9 on III, 12/11 on IV, 8/8 on V; subdigital lamellae of forelimb single, 6/6 on finger I, 11/12 on II, 15/16 on III, 16/16 on IV, 9/8 on V; subdigital lamellae on toes I and II single, on toe III paired on the middle, on toe IV paired except for a few ones, on toe V paired at the base; number of subdigital lamellae (pairs when applicable) 6/6 on toe I, 10/11 on II, 16/17 on III, 21/21 on IV, 12/12 on V; groin region with small keeled, imbricate scales; scales on dorsal surface of hind limbs keeled and imbricate; scales on ventral surface of hind limbs smooth; scales on posterior surface of thighs granular and on shanks striated and imbricate; femoral pores absent; preanal pores absent; cloacal plate paired, bordered by two scales anteriorly, smaller than cloacal scales.

Additional measurements (mm) and proportions of the holotype: HL 9.91; HW 6.95; ShL 3.9; AGD 25.6; TL/SVL 2.05; HL/SVL 0.21; HW/SVL 0.15; ShL/SVL 0.08; AGD/SVL 0.56.

**Coloration in preservative (Figs. 1 and 2):** Dorsum dark brown with a grayish brown vertebral stripe that is four scales broad at midbody, and extends from occiput onto tail; vertebral stripe wide anteriorly becoming slightly slender at midbody; dorsal surface of head brown, sides of head and body dark brown; two bright cream spots on each side above insertion of forelimbs; light stripe extending ventrolaterally from lips to insertion of hind limbs, white on lips and grayish brown along the body; a distinct diagonal white bar with dark edges on each side of the mandible, extending from the sixth infralabial onto the proximal pregular; dorsal surface of limbs dark brown with a cream stripe along the arms; gular region pale gray, chest and venter dark gray; ventral surface of tail dark gray.

**Coloration of holotype in life (Fig. 3A):** Similar to that in preservative, but the bright cream spots on each side above forelimbs are replaced by two black ocelli with red centers, and the sides of the base of the tail have scattered red flecks. The iris is light brown.



## A new species of Andean microteiid lizard

**Table 1.** Squamation characters of *Pholidobolus ulisesi*. Range, followed by mean  $\pm$  standard deviation, is given for quantitative characters (if applicable). \*Includes adults of both sexes and 10 juvenile specimens of undetermined sex.

| Characters  | <i>Pholidobolus ulisesi</i>                     |   |   |
|---|---|---|---|
|   | Males<br><i>n</i> = 5                           | Females<br><i>n</i> = 4                         | All specimens*<br><i>n</i> = 19                 |
| Dorsal scales between occipital and posterior margin of hind limb | 28–31<br>29.6 $\pm$ 1.14                        | 29–32<br>30.6 $\pm$ 1.14                        | 28–32<br>30.05 $\pm$ 1.13                       |
| Dorsal scale rows in a transverse line at midbody                 | 19–22<br>20.4 $\pm$ 1.14                        | 18–21<br>19.6 $\pm$ 1.34                        | 17–22<br>20.05 $\pm$ 1.43                       |
| Ventral scales between collar fold and preanals                   | 20–21<br>20.75 $\pm$ 0.5                        | 20–23<br>20.8 $\pm$ 1.3                         | 20–23<br>21.06 $\pm$ 0.87                       |
| Ventral scale rows in a transverse line at midbody                | 6   | 6–8<br>6.8 $\pm$ 1.1                            | 6–8<br>6.56 $\pm$ 0.92                          |
| Subdigital lamellae on Finger IV                                  | 15–16<br>15.6 $\pm$ 0.55                        | 15–17<br>15.8 $\pm$ 0.84                        | 11–18<br>15.05 $\pm$ 1.65                       |
| Subdigital lamellae on Toe IV                                     | 20–21<br>20.4 $\pm$ 0.55                        | 18–22<br>20.6 $\pm$ 1.52                        | 15–22<br>19.32 $\pm$ 1.95                       |
| Maximum SVL   | 45.52   | 57.46   | 57.46   |
| TL/SVL  | 1.92–2.28<br>2.12 $\pm$ 0.18<br>( <i>n</i> = 3) | 1.83–2.17<br>2.05 $\pm$ 0.19<br>( <i>n</i> = 3) | 1.83–2.28<br>2.05 $\pm$ 0.18<br>( <i>n</i> = 7) |

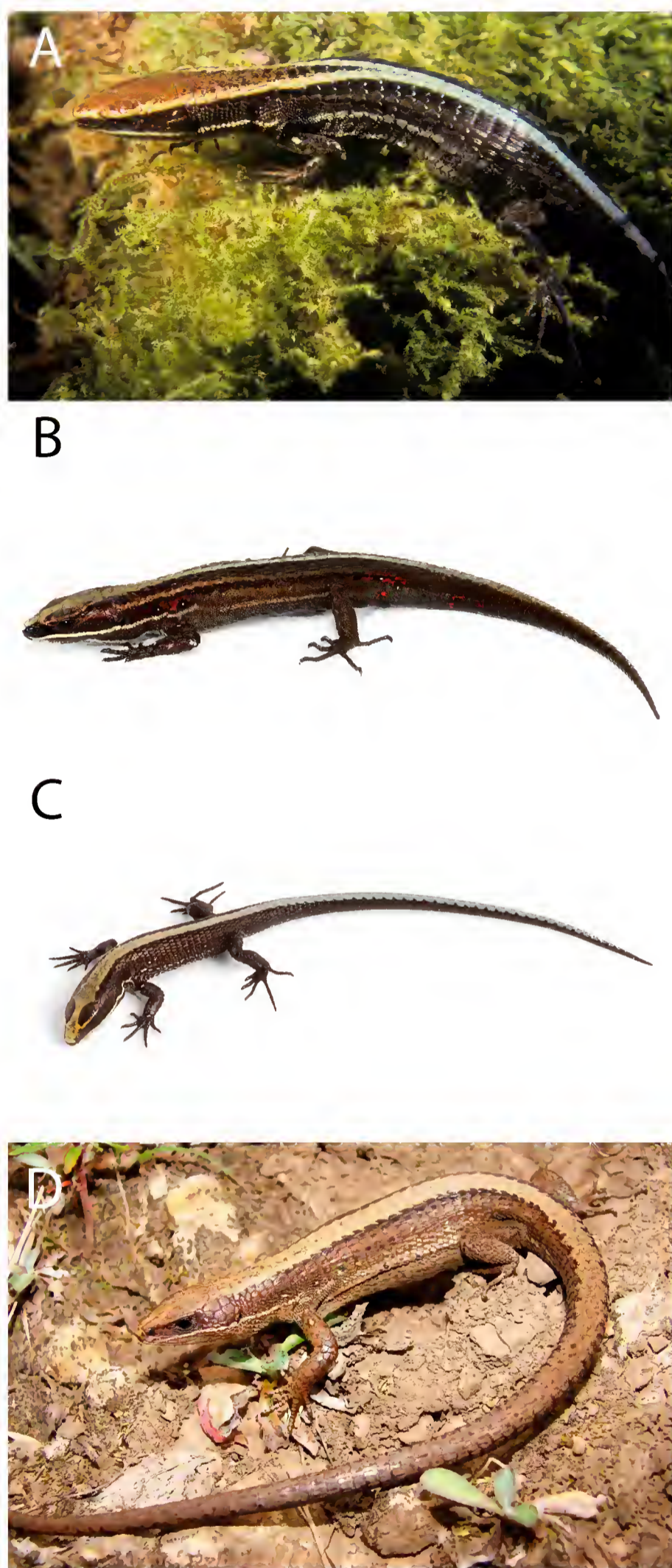


**Fig. 3.** Four individuals of *Pholidobolus ulisesi* sp. nov. in life. (A) holotype (CORBIDI 12734); (B) adult female (CORBIDI 12737); (C) juvenile (CORBIDI 12744); (D) adult male from Cañaris (photo voucher). Photographs by PJV.

**Variation:** Variation in measurements and scutellation of *Pholidobolus ulisesi* is presented in Table 1. Usually two supraoculars, 2/3 (left/right) in specimen CORBIDI 12742; superciliaries usually four, 3/4 in CORBIDI 12749, 6/5 in CORBIDI 00873, and 5/5 in CORBIDI 00872; little intrusive scales present on each side, in the posterior angle of frontonasal in three specimens (CORBIDI 12735, 12741, 12744); usually seven supralabials, 7/6 in CORBIDI 00871, 12738 and 6/6 in CORBIDI 12742–43; infralabials usually six, 5/5 in CORBIDI 12738, 12740, 12742, 6/5 in CORBIDI 00873, 12744

and 5/6 in CORBIDI 12735, 12743. Rows of ventrolateral keeled scales vary from two rows in nine specimens (56% of the type series), one row on each side in three specimens (CORBIDI 00872, 12741, and 12745), three rows on each side in one specimen (CORBIDI 12739), and absent in two adult specimens (CORBIDI 00871 and CORBIDI 00873). Usually two scales on posterior cloacal plate, only two specimens (CORBIDI 12737–38) have three scales, and two other specimens (CORBIDI 00871 and 00873) have four scales.





**Fig. 4.** Four species of *Pholidobolus*. (A) adult female of *P. dicrus* (QCAZ 5304); (B) adult male of *P. hillisi* (QCAZ 4999); (C) a juvenile of *P. vertebralis* (QCAZ 5082); (D) adult female of *P. sp.* from La Granja (CORBIDI 1678). Photographs by: (A) and (B) Santiago R. Ron, (C) OTC, and (D) PJV.

Males can be distinguished from females by having the contacted margins of rostral and mental distinctly dark brown or black (indistinct or not contrasting in females), and by the presence of red or orange spots above the insertion of forelimbs and on the sides of the base of tail (absent in females; Fig. 3B). Females are longer

(maximum SVL 57.4 mm,  $n = 4$ ) than males (maximum SVL 45.5 mm,  $n = 5$ ). Juvenile CORBIDI 12743 (Fig. 3C) differs from adults in having a fragmented dirty cream stripe along the flanks above the ventrolateral stripe.

**Hemipenial morphology:** The left hemipenis of the holotype of *Pholidobolus ulisesi* (Fig. 5) was everted during preservation and prepared posteriorly. The organ extends along approximately eight millimeters in length. The lobes of the organ are partially everted and the hemipenis is fully expanded. The hemipenial body is roughly conical in shape, with the basis distinctly thinner than the rest of the organ, and bears two small lobes with apical folds in the apex. The sulcus spermaticus is central in position, originating at the base of the organ, and proceeding in a straight line towards the lobes. The sulcus is broader in the region of the lobular crotch, where it is divided by a small fleshy fold; its branches lie on the medial region of the lobes, and end in their tips among folds. The sulcate face of the hemipenial body presents two nude areas parallel to the sulcus spermaticus that run along the entire hemipenial body.

The lateral and asulcate faces of the hemipenis are ornamented with a series of roughly equidistant flounces with calcareous spinules. Twenty-three rows of flounces extend along the body of the organ. There are four proximal rows restricted to a central position on the basal asulcate face of the hemipenis, all of them are roughly chevron-shaped. The four proximal flounces on the sides are diagonally positioned; the third to fifth flounces are separated from a complementary flounce positioned on the asulcate face and oriented in an inverse diagonal. The subsequent flounces towards the lobes cross the sides of the organ from the sulcate to the asulcate face, forming chevrons with vertices in the central region of each side pointing towards the basis of the organ. These chevron-shaped rows become reduced in size progressively towards the hemipenial apex. Similar to the description of the hemipenis of *Cercosaura vertebralis* by Uzzell (1973), the five distalmost lateral flounces of the hemipenis have an enlarged tooth in the vertex of the chevrons.

The lateral flounces are separated in two groups by a nude area in the central asulcate face that increases in size in the apical region, becoming Y-shaped. The region between the asulcate and lateral sides are marked by a conspicuous unevenness forming a distinctive bulge, which is also present in other species of the *Macropholidus* + *Pholidobolus* clade (*Macropholidus annectens*, *M. huancabambae*, *M. ruthveni*, *Pholidobolus affinis*, *P. hillisi*, *P. macbrydei*, *P. montium*, *P. prefrontalis*, *P. vertebralis*; Nunes, 2011; Torres-Carvajal et al. 2014).

The hemipenis of the holotype of *P. ulisesi* described herein (Fig. 5) is broadly congruent with the illustrated by Doan and Cusi (2014) for a specimen of *P. ulisesi*, considered by them as *P. vertebralis* (see “Discussion”



hereafter). Although Doan and Cusi (2014) reported a reduced count of flounces ornamenting the organ (14 versus 23 in the holotype of *P. ulisesi*), their Fig. 5B clearly shows at least 18 visible flounces ornamenting the hemipenis sides, plus other flounces not countable due the positioning of the organ and the lack of focus in some areas of the hemipenis photograph. Similar to the hemipenis of *P. ulisesi* described by Doan and Cusi (2014), but contrasting with the hemipenis of *P. vertebralis* illustrated by Hernández-Ruz and Bernal-González (2011) for a specimen from Nariño, Colombia, the hemipenis of the holotype of *P. ulisesi* presents the four flounces in basal position at the asulcate face separated from the other flounces ornamenting the hemipenis laterally. In the drawing presented by Hernandez-Ruz (2005) for *Cercosaura ampuedai* (synonym of *P. vertebralis* according to Doan and Cusi [2014]) such flounces are not visible, probably due the distally misplaced tie made during hemipenial preparation.

#### Distribution and natural history observations:

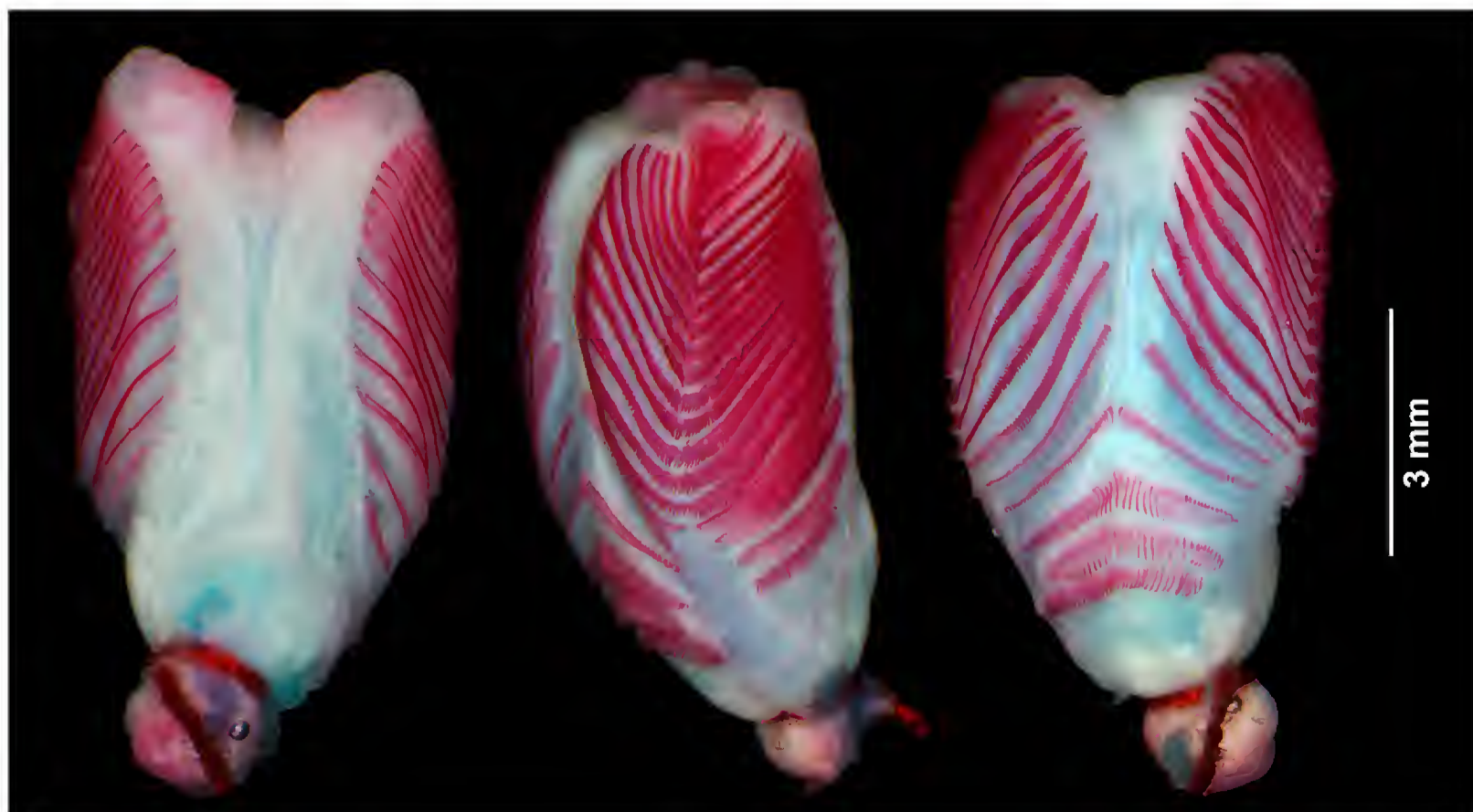
*Pholidobolus ulisesi* is known from five localities at elevations of 1,900–2,300 m in Cajamarca and Lambayeque departments, northern Peru (Fig. 6). All recorded localities lie within the Huancabamba depression, a region where the relatively low altitude of the Andean mountains causes fragmentation of montane habitats, and the northern extreme of the Central Andes at Cordillera Occidental in northern Peru. According to the terrestrial ecorregions of the world by Olson et al. (2001), *P. ulisesi* occurs within Eastern Cordillera real montane forest and Marañón dry forest.

*Pholidobolus ulisesi* was found during the day in sunny and cloudy conditions in secondary montane forest, in the edges of primary montane forest and recently opened areas for cattle ranching, as well as in small plantations

of bean and coffee. In the open cattle-ranching areas, *P. ulisesi* was found moving on fallen trees or hiding under trunks; in secondary montane forest, the lizards were found foraging within herbaceous vegetation and running through the patches of grass. They were especially abundant in coffee and bean plantations, where they were observed running through the herbaceous vegetation and hiding in leaf litter. Sympatric squamate reptiles collected with *P. ulisesi* were *Chironius monticola* and *Dipsas peruana* at El Chaupe and Huamantanga, and *Chironius monticola*, *Epictia teaguei*, *Erythrolamprus taeniurus*, *Micrurus peruvianus*, *Stenocercus arndti*, *S. huancabambae*, and *S. stigmatosus* at Quebrada La Iraca.

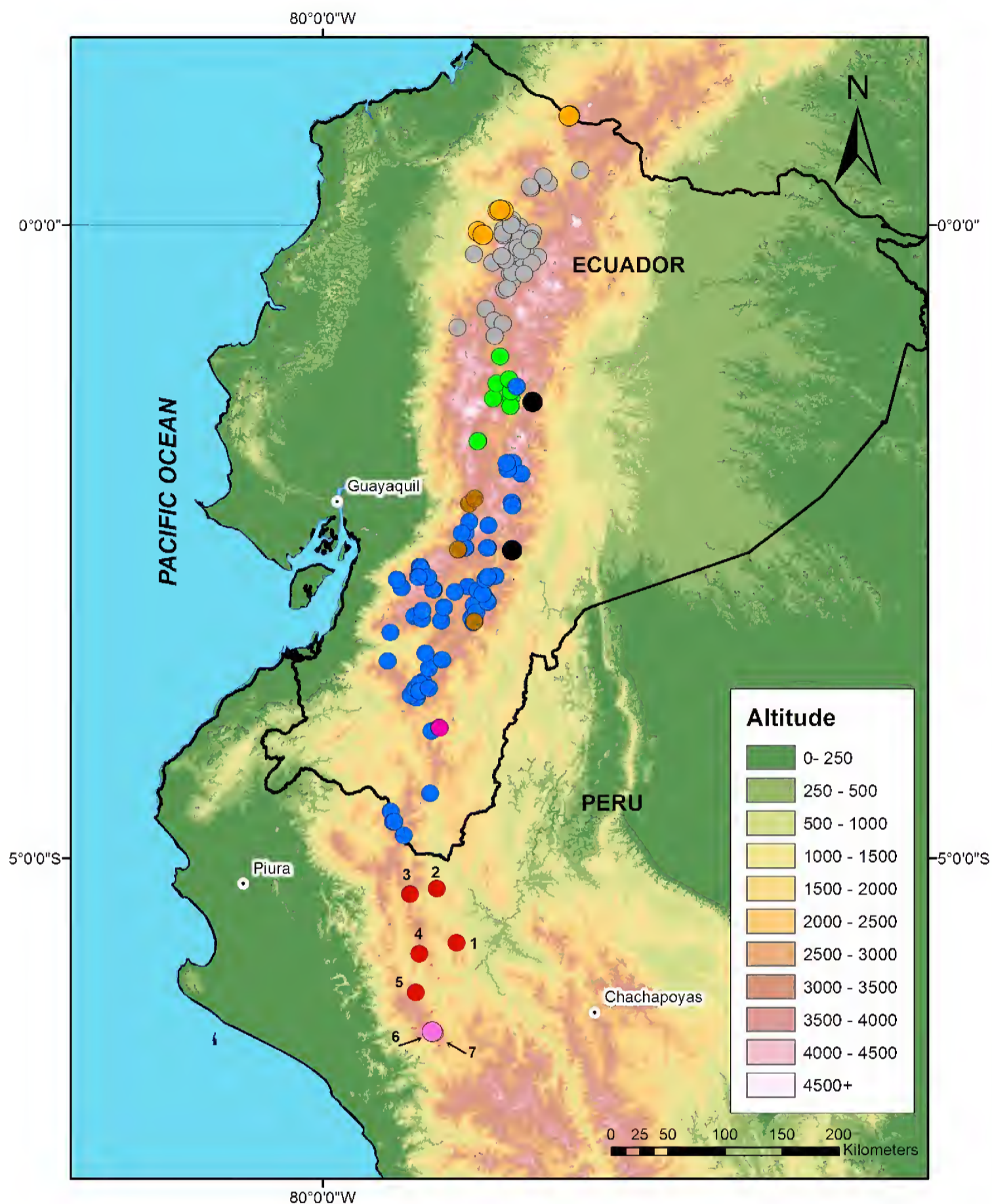
**Etymology:** The specific epithet “*ulisesi*” is a noun in the genitive case and a patronym for Ulises Gamonal Guevara, for his significant contribution to the archaeology of Cajamarca in northwestern Peru. One of his major contributions is the discovery of the >6,000-year-old Fajal cave paintings in San Ignacio, declared as Cultural Patrimony of the Nation.

**Remarks:** In a molecular phylogeny of *Cercosaura* and related taxa, Torres-Carvajal et al. (2015) showed, with high support, that *Pholidobolus ulisesi* (*Pholidobolus* sp. in their paper) and *P. hillisi* are sister species. Together they form a clade sister to all other species of *Pholidobolus*. In addition, these authors found that both “*Cercosaura*” *vertebralis* and “*Cercosaura*” *dicra* were nested within *Pholidobolus*, and were therefore referred to this genus (Torres-Carvajal et al. 2015). An identical topology can be observed in a recent molecular phylogeny of the clade Cercosaurinae by Torres-Carvajal et al. (2016). Therefore, we adopt this taxonomic change in the discussion below.



**Fig. 5.** Left hemipenis of *Pholidobolus ulisesi* sp. nov. (CORBIDI 12734 - holotype) in sulcate (**left**), lateral (**middle**), and asulcate (**right**) views. Photographs by PMSN.





**Fig. 6.** Distribution of *Pholidobolus* in Ecuador and Peru (circles): *P. affinis* (green); *P. dicrus* (black); *P. hillisi* (purple); *P. macbrydei* (blue); *P. montium* (gray); *P. prefrontalis* (brown); *P. ulisesi* sp. nov. (red); *P. vertebralis* (orange); and *P. sp.* (pink). Localities for *P. ulisesi* are: (1) Bosque de Huamantanga (type locality); (2) El Chaue; (3) Estación Biológica Chichilapa in the Santuario Nacional Tabaconas Namballe, taken from Doan and Cusi (2014); (4) San Felipe de Jaén; (5) Cañaris; (6) Quebrada La Iraca (near La Granja village); and (7) Quebrada Checos (near La Granja village) taken from Doan and Cusi (2014).

## Discussion

*Pholidobolus vertebralis* has been repeatedly reported for Peru based on misidentified specimens. Uzzell (1973) reported one specimen (LACM 58811) of this species (as *Prionodactylus vertebralis*) from Piura, 11 miles E of Canchaque, on the western slope of the Huancabamba Mountains. He noted, however, that this specimen was different morphologically from other specimens of *P. vertebralis*. Doan and Cusi (2014) confirmed this specimen as *P. vertebralis* even though they also noted important morphological differences with other specimens,

such as the absence of prefrontal scales, an undivided palpebral disk, and the absence of a light vertebral stripe. After reviewing several specimens of *C. vertebralis* from Ecuador ( $n = 22$ ; see Appendix 1), we found that all have prefrontal scales, a divided palpebral disk, and a light vertebral stripe (“*vertebralis*” refers to that stripe). Based on photographs of specimen LACM 58811, as well as its examination by staff of the herpetological collection at the Natural History Museum of Los Angeles County, we were able to identify it as *Macropholidus huancabambae* Reeder 1996. Besides the differences between this specimen and other specimens of *P. vertebralis* noted by



**Key to species of *Pholidobolus***

- 1a. Loreal scale usually present and frequently in contact with supralabials; dorsals striated; conspicuous light vertebral stripe absent..... 2
- 1b. Loreal scale present, not in contact with supralabials; dorsals keeled; conspicuous light vertebral stripe present..... 5
  
- 2a. Prefrontal scales present..... 3
- 2b. Prefrontal scales absent..... 4
  
- 3a. Ocelli on flanks present, supraoculars three..... *P. affinis*
- 3b. Ocelli on flanks absent, supraoculars two..... *P. prefrontalis*
  
- 4a. Sexual dimorphism strong, with males having distinctly broader heads and colorful flanks (red stripes and white flecks)..... *P. macbrydei\**
- 4b. Sexual dimorphism not very marked, with males having slightly broader heads and inconspicuously colored flanks (different tones of brown stripes)..... *P. montium*
  
- 5a. Prefrontal scales absent..... 6
- 5b. Prefrontal scales present..... 7
  
- 6a. Diagonal white bar along rictal region, extending from the posteriormost infralabial to the proximal preangular..... *P. ulisesi*
- 6b. Diagonal white bar in the rictal region absent..... *P. sp.*
  
- 7a. Vertebral stripe bifurcates anteriorly at midbody..... *P. dicrus*
- 7b. Vertebral stripe straight, not bifurcated..... 8
  
- 8a. Diagonal white bar in the rictal region, extending from the proximal preangular to the forelimb..... *P. hillisi*
- 8b. Diagonal white bar in the rictal region absent..... *P. vertebralis*

\*We observed some specimens of *Pholidobolus macbrydei* with small loreal scales, not contacting supralabials, as well as specimens lacking a loreal scale.

Uzzell (1973) and Doan and Cusi (2014), the dorsal and flank scales are similar in size, whereas in *P. vertebralis* flank scales are noticeably smaller than dorsals.

Doan and Cusi (2014) also reported two new localities for *Pholidobolus vertebralis* in Peru based on misidentified specimens of *P. ulisesi* and an undescribed species of *Pholidobolus*. These localities lie in the Cajamarca department, one in the Tabaconas Namballe Natural Sanctuary (*P. ulisesi*) and the other in Quebrada Checos, approximately one km away from La Granja village (*P. sp.*) (see Fig. 6). Although *P. ulisesi* is similar to *P. vertebralis* (Fig. 4C) in having a dark brown dorsum with a conspicuous narrow middorsal pale stripe, and a white labial stripe that extends posteriorly as a cream or pale brown stripe along the ventrolateral region, it differs from *P. vertebralis* (character states in parenthesis) in lacking prefrontal scales (prefrontals present), and in having a diagonal white bar in the rictal region (rictal bar absent); ocelli above forelimbs and along the sides of the base of tail (ocelli also present along the flanks); a cream stripe along the forearm (stripe absent, one or two ocelli along the forearm); a gray venter in adults of both sexes in preservative (creamy gray with dark gray reticulations

or dark gray with pale marks); middorsal stripe between 3–4 scales wide at midbody (only two scales wide); and slender hemipenial body (robust). In addition, *P. ulisesi* is smaller than *P. vertebralis*, with a maximum SVL of 45.5 mm in males ( $n = 5$ ) and 57.4 mm in females,  $n = 4$  (males 58.9 mm,  $n = 5$ , and females 68.4 mm,  $n = 5$ ). The specimens of *Pholidobolus sp.* from Quebrada Checos reported by Doan and Cusi (2014), and a specimen examined by us from Quebrada la Iraca, both localities approximately two km apart, can be easily distinguished from *P. vertebralis* by lacking prefrontal scales, and from *P. ulisesi* by lacking the rictal diagonal white bar and a white stripe on the forearm. We acknowledge that the differences in color pattern between *P. ulisesi* and *P. sp.* might only represent interpopulational variation within *P. ulisesi*, which should be addressed with the examination of further specimens, as well as phylogenetic analyses of molecular data.

In conclusion, there are no voucher specimens of *Pholidobolus vertebralis* from Peru, and its presence in this country has been based on misidentified specimens of *Macropholidus huancabambae*, *P. ulisesi*, and an undescribed species of *Pholidobolus*. Furthermore, we also



examined the single specimen of *P. vertebralis* reported by Uzzell (1973) from southwestern Ecuador (AMNH 18312) and conclude that it represents another undescribed species of *Pholidobolus*. Thus, the southernmost records of *P. vertebralis* are from northwestern Ecuador around its type locality (Intag, Imbabura province). Finally, as noted by Uzzell (1973), the few records of *P. vertebralis* east of the Andes in Ecuador are most likely based on erroneous locality data, as has been noted for other species of amphibians and reptiles from the same localities (e.g., Uzzell 1973).

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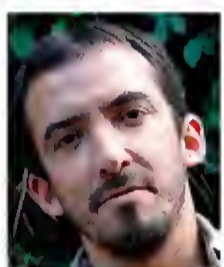
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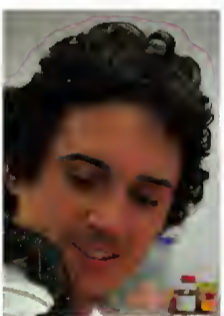
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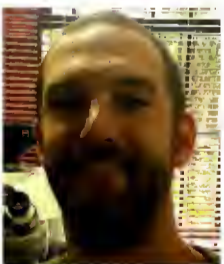
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## Appendix 1

### Additional specimens examined

*Macropholidus huancabambae*.—PERU: Piura: 11 miles E of Canchaque, on the western slope of the Huancabamba Mountains, LACM 58811.

*Pholidobolus affinis*.—ECUADOR: Provincia Chimborazo: Colta, 1°41'56"S, 78°46'25"W, 3,215 m, QCAZ 9899–01; Sicalpa, 1°42'18"S, 78°46'32"W, 3,212 m, QCAZ 11887. Provincia Cotopaxi: Cutuchi river, San Miguel de Salcedo, 1°2'9"S, 78°35'53"W, 2,640 m, QCAZ 9641. Provincia Tungurahua: six km N Mocha to 400 m Panamerican Highway, 1°22'1"S, 78°39'16"W, 3,205 m, QCAZ 9895–97; Ambato surroundings, 1°14'59.8"S, 78°37'33"W, QCAZ 9340–73, 9375–9443; Chamisa on road to Guadalupe, 1°21'44"S, 78°30'39"W, 2,348 m, QCAZ 7266; Cotaló on path to Mucubi Community, 1°25'46"S, 78°31'3"W, 2,626 m, QCAZ 9839; Patate, 1°18'42"S, 78°30'36"W, 2,199 m, QCAZ 9847–50; Poatug Hamlet, Aya Samana, 1°16'58"S, 78°29'29"W, 2,573 m, QCAZ 10005, 10008, 10011–13, 10016, 10018; Poatug Hamlet, Terremoto, 1°16'23"S, 78°29'29"W, 2,547 m QCAZ 9997–10000, 10002–10004; San Miguelito on path to Pillaro, 1°13'12"S, 78°31'31"W, 2,689 m, QCAZ 9844; San Miguelito on path to Terán, 1°12'58"S, 78°31'42"W, 2,741 m, QCAZ 9843.

*Pholidobolus dicrus*.—ECUADOR: Provincia Morona Santiago: Guarumales, 2°34'0.0006"S, -78°30'0"W, 1,700 m, QCAZ 5292, 5304. Provincia Tungurahua: Río Blanco, Vía Baños-Puyo, 1°23'55.6434"S, 78°20'24"W, 1,600 m, QCAZ 6936, no locality data QCAZ 8015.

*Pholidobolus hillisi*.—ECUADOR: Provincia Zamora-Chinchi: near San Francisco Research Station on Loja-Zamora road, 3°57'57"S, 79°4'45"W, WGS84, 1,840 m, QCAZ 4998–99, 5000; San Francisco Research Station, 3°58'14"S, 79°4'41"W, 1,840 m, QCAZ 6840, 6842, 6844.

*Pholidobolus macbrydei*.—ECUADOR: Provincia Azuay: 10 km S Cutchil, 3°8'2"S, 78°48'47"W, 2,900 m, QCAZ 823–24; 1.2 km E Osoranco, 2°46'8"S, 78°38'10"W, 2,390 m, QCAZ 826; 6.2 km S Cutchil, 3°6'32"S, 78°48'4"W, 2,800 m, QCAZ 827; 20 km NE Cuenca, 2°51'0"S, 78°51'14"W, QCAZ 1359; seven km Sigsig, 2°59'56"S, 78°48'25"W, 2,890 m, QCAZ 1537; 6 km S Oña, 3°29'49"S, 79°9'47"W, QCAZ 3658; 20 km Cuenca-El Cajas, 2°46'39"S, 79°10'12"W, 3,508 m, QCAZ 9932–34, 9936–38, 10020; Cochapamba, 2°47'50"S, 79°24'56"W, 3,548 m, QCAZ 10133–35; Cochapata, 3°25'47"S, 79°3'35"W, 3,074 m, QCAZ 12605–07; Cuenca, Cuenca-Azoguez Panamerican Highway 2°53'43"S, 78°57'30"W, 2,486 m, QCAZ 6985; El Cajas National Park, path to Patul Community, 2°44'28"S, 79°14'5"W, 4,092 m, QCAZ 8010–11; El Cajas National Park, Patul river, 2°41'37"S, 79°13'56"W, 3,610 m, QCAZ 8893; El Cajas National Park, Zhurcay river, 3°2'30"S, 79°12'56"W, 3,766 m, QCAZ 8900–01; El Cajas National Park, 2°42'21"S, 79°13'32"W, 3,600 m, QCAZ 8946; El Capo, 2°46'43"S, 79°14'43"W, 4,100 m, QCAZ 4997; Girón, San Gregorio Community, Quinsacocha paramo, 3°6'22"S, 79°13'4"W, 3,242 m, QCAZ 8510–11; Girón, San Gregorio Community, Quinsacocha paramo, 3°2'30"S, 79°12'56"W, 3,766 m, QCAZ 8894–99, 8902–05, 8907; Girón, San Gregorio Community, Quinsacocha paramo, 3°2'30"S, 79°12'57"W, 3,766 m, QCAZ 8906; Guablid, 2°46'30"S, 78°41'51"W, 2,453 m, QCAZ 9913–17, 9919–20, 9940–41; Gualaceo-Limón road, 2°56'53"S, 78°42'43"W, 3,110 m, QCAZ 819–22; Gualaceo-Limón road, 8.1 km O Azuay-Morona Santiago border, 2°57'50"S, 78°42'7"W, 3,140 m, QCAZ 825; Gualaceo, 2°52'56"S, 78°46'31"W, 2,298 m, QCAZ 9606; Gualaceo-Plan de Milagro road, 2°54'35"S, 78°44'4"W, 2,624 m, QCAZ 10875; Las Tres Cruces, 2°46'30"S, 79°14'53"W, QCAZ 4136; Maylas, Gualaceo-Macas road, 2°58'25"S, 78°41'41"W, 3,100 m, QCAZ 7269; Mazán Protected Forest, 2°52'29"S, 79°7'26"W, 2,700 m, QCAZ 1296–97; Mazán Protected Forest, 2°52'31"S, 79°7'45"W, 3,189 m, QCAZ 8008, 8013; Oña-La Paz road, 3°22'42"S, 79°11'20"W, 2,969 m, QCAZ 6031; Patacocha hill, 3°7'16"S, 79°3'54"W, 3,340 m, QCAZ 6144; Pucara, Tres Chorreras, 3°12'49"S, 79°28'3"W, QCAZ 11038; Quinoas river, 3°5'14"S, 79°16'40"W, 3,200 m, QCAZ 1564–66; San Antonio, 2°51'40"S, 79°22'43"W, 2,943 m, QCAZ 9668; San Vicente-Cruz path, 2°47'43"S, 78°42'53"W, 3,044 m, QCAZ 11416–17, 11420; Sigsig, 3°7'46"S, 78°48'14"W, 2,969 m, QCAZ 5605–08; Sigsig road, 3°3'17"S, 78°47'19"W, 2,574 m, QCAZ 9605; Tarqui, 3°0'57"S, 79°2'40"W, 2,627 m, QCAZ 8512. Provincia Cañar: Cañar, 2°33'39"S, 78°55'51"W, QCAZ 9947; Culebrillas, 2°25'35"S, 78°52'12"W, 4,000 m, QCAZ 1349; Guallicanga ravine, 2°25'56"S, 78°54'8"W, 3,960 m, QCAZ 10048–49; Guallicanga river, 2°28'24"S, 78°58'22"W, 3,048 m, QCAZ 10051–52; Ingapirca, 2°32'43"S, 78°52'28"W, 3,400 m, QCAZ 1551; Juncal, 2°28'24"S, 78°58'22"W, 3,048 m, QCAZ 10050; Mazar Protected Forest, 2°32'48"S, 78°41'54"W, QCAZ 7376–84, 7883; Mazar Reserve, La Libertad, 2°32'45"S, 78°41'46"W, 2,842 m, QCAZ 10970–72. Provincia Chimborazo: Alao, 10 km Huamboya, 1°52'22"S, 78°29'51"W, 3,200 m, QCAZ 1567–68; Atillo Grande, Magdalena lake, 2°11'15"S, 78°30'25"W, 3,556 m, QCAZ 9214; Atillo Grande, Frutatián lake, 2°12'57"S, 78°30'5"W, 3,700 m, QCAZ 9216–18; Culebrillas, Sangay National Park, 1°57'39"S, 78°25'55"W, 3,345 m, QCAZ 9612; Pungalá, Etén Community, Timbo, 1°55'45"S, 78°32'14"W, 3,408 m, QCAZ 9616–21; Pungalá, Melán Community, 1°52'30"S, 78°32'52"W, 3,564 m, QCAZ 9626–29, 9631; Ozogoché, 2°22'7"S, 78°41'20"W, 4,040 m, QCAZ 6006–07; Shulata, 2°20'22"S, 78°50'36"W, 3,228 m, QCAZ 5597–98. Provincia El Oro: Guanazán, 3°26'24"S, 79°29'13"W, 2,638 m, QCAZ 7891, 7894. Provincia Loja: 17.1 km S Saraguro, 3°43'45"S, 79°15'53"W, 3,150 m, QCAZ 828; 26 km N Loja, Huashapamba Native Forest, 3°39'30"S, 79°16'20"W, 2,894 m, QCAZ 8651; Cordillera of Lagunillas, Jimbura, 4°49'1"S, 79°21'43"W, 3,600 m, QCAZ 3785; Cordillera of Lagunillas, Jimbura, 4°37'42"S, 79°27'49"W, 3,450 m, QCAZ 6145–47; Fierro Urco, 3°42'38"S, 79°18'18"W, 3,439 m, QCAZ 6949–50; Gurudel, 3°39'22"S, 79°9'47"W, 3,100 m, QCAZ 5078–79; Jimbura, Jimbura lake, 4°42'32"S, 79°26'48"W, 3,036 m, QCAZ 6945–48; Jimbura, path to Jimbura lake, 4°42'34"S, 79°26'8"W, 3,348 m, QCAZ 10054–62; Military antenna, Saraguro, 3°40'46"S, 79°14'16"W, 3,190 m, QCAZ 3673–75, 9632; San Lucas, 3°43'55"S, 79°15'38"W, 2,470 m, QCAZ 2861; Saraguro, 3°37'13"S, 79°14'9"W, 3,100 m, QCAZ 3606, 3754; Urdaneta, 3°36'6"S, 79°12'31"W, QCAZ 2019. Provincia Tungurahua: Poatug Hamlet, El Corral, 1°16'21"S, 78°28'5"W, 3,468 m, QCAZ 8047, 9995–96. Provincia Zamora-Chinchi: Loja-Podocarpus National Park road, 3°59'44"S, 79°8'28"W, 2,776 m, QCAZ 10870–71; Valladolid, Podocarpus National Park, 4°29'3"S, 79°8'56"W, 1,800 m, QCAZ 3743.

*Pholidobolus montium*.—ECUADOR: Provincia Cotopaxi: two km S Chugchilán on road to Quilotoa, 0°48'24"S, 78°56'11"W, 2,917 m, QCAZ 8056–58; Latacunga, 0°52'27"S, 78°38'26"W, 2,857 m, QCAZ 873–74, 1411–12, 9642; Mulaló, 0°46'35"S, 78°34'40"W, 3,030 m, QCAZ 9639; San Juan de Pasto Calle, 0°45'4"S, 78°38'51"W, 1,956 m, QCAZ 8053–54; South Illiniza, 0°39'43"S, 78°42'40"W, 3,400 m, QCAZ 858–59, 1454. Provincia Imbabura: Atuntaqui, 0°19'59"N, 78°12'50"W, QCAZ 855; Cotacachi, Peribuela, Cuicocha Lake, Cotacachi-Cayapas Reserve, 0°17'34"N, 78°21'5"W, 3,082 m, QCAZ 9683, 9685–86; 0°23'4"N, 78°15'25"W, 2,900 m, QCAZ 6137, 6139; Cotacachi-Cayapas Reserve, José María Yerovi Islets, 0°18'20"N, 78°21'41"W, 3,093 m, QCAZ 10959–60; El Juncal, 0°26'6"N, 77°57'58"W, QCAZ 6451. Provincia Pichincha: 16 km W Chillogallo, Quito-Chiriboga road, 0°17'46"S, 78°39'30"W, 3,100 m, QCAZ 797; five km E Pifo-Papallacta road, 0°15'3"S, 78°17'58"W, 2,800 m, QCAZ 1107–08; Alambi, 0°1'59"S, 78°34'26"W, 2,727–3,800 m, QCAZ 9691; Alangasí, 0°18'24"S, 78°24'40"W, QCAZ 1453, 1469; Amaguaña, Hacienda San Ignacio, 0°22'22"S, 78°30'14"W, QCAZ 1463–64, 5275; Calacalí, Simón Bolívar Street, uphill through secondary road, 0°1'1"N, 78°30'49"W, 3,001 m, QCAZ 11674, 11676, 11678–79; Calacalí Stadium, 0°0'0.3"S, 78°30'38"W, 2,833 m, QCAZ 11682; Carretas, 0°6'25"S, 78°26'46"W, QCAZ 875; Chillogallo, 0°16'48"S, 78°33'25"W, QCAZ 840–43; Cumbayá, La Primavera, 0°12'6"S, 78°25'40"W, QCAZ 7248; Guayllabamba, 0°3'23"S, 78°20'26"W, QCAZ 7905; Inga, 5.5 km SE La Merced, 0°17'51"S, 78°20'52"W, 2,798 m, QCAZ 5278; Lloa, 0°14'52"S, 78°34'33"W, QCAZ 4109; Lloa Stadium, 0°14'39"S, 78°35'12"W, 3,059 m, QCAZ 11661; Loreto, road to Molinuco, Central Stadium,



## Appendix 1 (continued) Additional specimens examined

0°23'4"S, 78°24'30"W, 2,844 m, QCAZ 11663; Machachi, 0°29'50"S, 78°32'25"W, QCAZ 844–48, 1374–77, 1462; Machachi, The Tesalia Springs Company S.A. surroundings, 0°30'27"S, 78°33'57"W, 2,900 m, QCAZ 1465–67, 830–31, 833, 860–61, 1459–61; Nono, 0°4'42"S, 78°34'24"W, 2,843 m, QCAZ 11653–55; Nono School, 0°4'4"S, 78°34'35"W, 2,754 m, QCAZ 11656–58; Pasochoa, 0°26'24"S, 78°30'15"W, 2,850 m, QCAZ 1451–52; Pomasqui, 0°3'3"S, 78°27'21"W, QCAZ 862–68; Pululahua Volcano, 0°2'34"N, 78°30'15"W, QCAZ 1450, 1520; Quito, Bellavista, 0°11'21"S, 78°28'35"W, QCAZ 1099; Quito, Chillogallo, 0°16'26"S, 78°33'23"W, QCAZ 8967; Quito, Itchimbía, 0°13'21"S, 78°29'56"W, QCAZ 834, 1455–58, 1643, 2843; Quito, Garden of the Pontificia Universidad Católica del Ecuador (PUCE), 0°12'33"S, 78°29'28"W, 2,800 m, QCAZ 856–57, 7032, 1295, 2853; Quito, Parque Metropolitano, 0°10'35"S, 78°27'40"W, QCAZ 4051; Quito, Universidad Central del Ecuador, 0°11'59"S, 78°30'19"W, 2,800 m, QCAZ 3727; Río Guajalito Protected Forest, 0°13'44"S, 78°48'22"W, QCAZ 1338–39; San Antonio de Pichincha, 0°0'33"S, 78°26'45"W, QCAZ 580–81, 790–92, 849, 1119–20, 1368, 1393, 2220, 2223, 2653; Tababela, International Airport, 0°6'21"S, 78°21'4"W, QCAZ 8046, 9044, 10064, 10974–76; Quito, Tumbaco, 0°12'34"S, 78°24'2"W, QCAZ 1113–14; Uyumbicho, 0°22'59"S, 78°31'6"W, QCAZ 870.

*Pholidobolus prefrontalis*.—ECUADOR: Provincia Azuay: Sigsig, 3°7'46"S, 78°48'14"W, 2,480 m, QCAZ 1553; Provincia Cañar: Cañar, 2°33'29"S, 78°56'4"W, QCAZ 1410; Provincia Chimborazo: Alausí, 2°11'54"S, 78°50'42"W, 2,359 m, QCAZ 9907–9911; Tixán, 2°9'22"S, 78°48'3"W, 2,908 m, QCAZ 9951–54; Tixán, 2°9'22"S, 78°48'3"W, 2,908 m, QCAZ 9951–54.

*Pholidobolus vertebralis*.—ECUADOR: Provincia Carchi: Chilma Bajo, 0°51'53.83" N, 78°2'59.26" W, 2,071 m, QCAZ 5057, 8671–8673, 8678, 8679, 8717, 8724, 0°51'50.31" N, 78°2'50.05" W, 2,022 m, QCAZ 8684–8689. Provincia Pichincha: Mindo, 0°3'2.41" S, 78°46'18.77" W, 1,700 m, QCAZ 2911, 2912, 2915, 0°4'40.98"S, 78°43'55.02"W, 1,601 m, QCAZ 7528; Cooperativa El Porvenir, El Cedral 0°6'50.40" N, 78°34'11.75" W, 2,297 m, QCAZ 5081, 5082; Santa Lucía de Nanegal, 0°6'48.70"N, 78°36'48.60"W, 1,742 m, QCAZ 10667, 0°7'8.51"N, 78°35'58.70"W, 1,900 m, QCAZ 10750. LOCALITY IN ERROR: ECUADOR: Provincia Pastaza: Mera, AMNH 60586–97.

*Pholidobolus* sp.—ECUADOR: Provincia El Oro: El Chiral, 1,350 m, AMNH 18312.

*Pholidobolus* sp.—PERU: Cajamarca: Provincia de Chota: Quebrada La Iraca (near to La Granja village), 6°22'09.9"S, 79°08'04.61"W, 2,213 m, CORBIDI 1679.

In accordance with the International Code of Zoological Nomenclature new rules and regulations (ICZN 2012), we have deposited this paper in publicly accessible institutional libraries. The new species described herein has been registered in ZooBank (Polaszek 2005a, b), the official online registration system for the ICZN. The ZooBank publication LSID (Life Science Identifier) for the new species described here can be viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/." The LSID for this publication is: urn:lsid:zoobank.org:pub:CAB026AC-B1CE-4F43-B0C3-AB908645159F.

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### Citations

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